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Synthesis of knowledge on treehoppers from French Guiana (Hemiptera: Membracidae, Aetalionidae). Part II : biology, host-plants, and interactions

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Abstract. – This article reports on the knowledge of host plants and mutualistic interactions of membracids in French Guiana, based on six years of field surveys conducted between 2016 and 2023. Brief notes are presented regarding microhabitats, phenology, polyphagy, predation, and parasitism. Several hypotheses are proposed to explain evolutionary convergences and defense mechanisms. Additionally, a classification approach for membracids is introduced, based on ecological traits (degree of association with ants) and morphological characteristics (mimicry, shape of pronotal helmets).

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Introduction

Membracids (Hemiptera: Membracidae) constitute a fascinating and atypical family of insects, notable for several unique biological and ecological characteristics. Their morphological diversity, evident both at the larval and adult stages, is particularly remarkable and reflects a wide range of adaptive strategies. Moreover, this family is characterised by rare behaviours among insects. Certain species, for example, provide maternal care such as egg brooding and larval attendance until maturity. From an ecological interaction perspective, most gregarious species maintain close mutualistic relationships with ants, whereas solitary species exhibit more moderate interactions with these hymenopterans.

Scientific interest in membracids is longstanding and has prompted numerous entomological studies that have enhanced understanding of membracids ecology. In particular, researches have studied membracids relationships with host plants, mutualistic interactions, predation strategies, life cycles, and communication modes (Cocroft, 2001, 2002, 2003). Major contributions to the knowledge of Neotropical membracids in the twentieth century include pioneering works by Haviland (1925), Richter (1942a, 1942b, 1942c), Tode (1966), Wood (1984, 1990, 1999), as well as Dietrich and Deitz (1991). Additionally, Godoy et al. (2006) synthesized available ecological data, while Florez-V (2015) produced a

comprehensive monograph on Colombian membracids, integrating mutualistic interactions and host plants, enriched by original observations.

Regarding French Guiana, research on membracids remains fragmented and limited. Only a few sporadic studies have been conducted, notably by Boulard (1980, 1983, 1991), along with recent contributions incorporating ecological data within taxonomic works by Lapèze (2022, 2024). This gap highlights a significant lack of in-depth knowledge concerning the diversity, ecology, and interactions of membracids in this region. The present article continues from the previous publication entitled « Synthèse des connaissances sur les membracides et les aetalions de Guyane française (Hemiptera : Auchenorrhyncha : Membracidae, Aetalionidae). Partie I : historique et liste des espèces recensées. ». This effort stems from the first author's intention to substantially improve understanding of Guyanese membracids by providing a more comprehensive and updated analysis of their ecology and interactions. The objective of this study is therefore to address the identified gaps by offering a detailed and critical synthesis of existing data, while proposing new avenues for understanding the ecological dynamics of these insects within Neotropical forest ecosystems. It is anticipated that this research will contribute to enriching the knowledge base necessary for the conservation and sustainable management of forest habitats in French Guiana.

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Material and methods

The study was conducted in French Guiana, a region characterized by an annual rainfall ranging between 2,500 and 3,500 mm, with a pronounced rainy season from December to July, and an average annual temperature of 26–28 °C. The terrain is generally gently undulating, dominated by coastal plains, hilly areas, and higher granite massifs reaching up to 800 meters inland.

The forest habitats of French Guiana are highly diverse and can be classified according to the Catalogue des habitats forestiers de Guyane (Guitet et al., 2018). These include coastal environments such as mangroves occupying intertidal zones, littoral forests, and coastal shrub formations. Riparian habitats are characterized by alluvial and swamp forests along waterways. Roadside and trail-edge formations, characterised by open or regenerating environments, favour certain pioneer plant species. Interior forests comprise several types: dense evergreen forests on hydromorphic soils, forests on well-drained ferrallitic soils, forests on granite or schist substrates, as well as lower montane forests in higher massifs.

The prospections were primarily conducted in forest habitats along the coast accessible via forest tracks, as well as interior forests near villages. Savannas and mangroves remain particularly under-sampled due to the difficulty of access and the relatively low plant diversity, which suggests the presence of a fauna that is original but much less diverse compared to the forest block.

This ecological diversity offers a wide range of niches for tropical fauna and flora, notably for the insects targeted in this study, the membracids. The data presented here derive from visual surveys, light-attraction traps, and interception traps of the Malaise type, conducted in French Guiana from 2016 to 2023, mainly by the first author. These surveys were carried out as part of inventory missions for the *Société Entomologique Antilles-Guyane* or opportunistically during unrelated field missions, but in both cases always focusing specifically on membracids.

Visual surveys consisted of meticulous observation of vegetation, primarily at forest edges, clearings, and trail margins, with particular attention to tender shoots. The interception or Malaise trap is a passive device composed of a vertical fabric panel (mosquito net type) installed perpendicular to insect flight corridors. Further details are provided in Lapèze (2024). Membracids encountered during visual surveys were photographed along with their host plants and any interacting organisms (in cases of predation, parasitism, or mutualism). The presence of nymphs or egg clutches was also recorded. These observations were subsequently entered into the database. Specimens deemed of interest for the collection were captured using a tube pre-filled with fabric soaked in ethyl acetate or ethanol. All collected specimens were mounted either glued on card points or double-mounted on minuten pins, then stored in the reference collection (Collection Jérémie Lapèze, Kourou, French Guiana).

Membracid identifications were performed by Jérémie Lapèze based on examination of specimens in the collection or directly in the field, with support from specialist colleagues for certain species (see acknowledgments). Botanical identifications were primarily based on photographs by Giacomo Sellan. Some identifications were made by Olivier Gaubert from photographs, or by Coralie Dalban-Pilon from samples or photographs. The most common and frequently encountered plant species during surveys were identified directly in the field by Jérémie Lapèze. Ant identifications were carried out by Baptiste Bentameur and Alex Salas-Lopez based on photographs, or by Jérémie Lapèze directly in the field for species presumed unmistakable and common, such as *Ectatomma tuberculatum*, *Daceton armigerum*, and *Cephalotes atratus*.

Results and Discussion

Out of the 302 Membracidae species recorded in French Guiana, only 151 species (i.e., 50%) were observed during visual surveys; the remaining species were detected exclusively through light traps or Malaise interception traps. These figures are slightly biased by the fact that the list presented in this article includes only identified and catalogued species, excluding those currently under determination or description, which represent a substantial portion of the diversity. According to the latest estimates, combining collection data and molecular analyses highlighting species complexes, French Guiana harbours a minimum of 500 Membracidae species and 12 Aetalionidae species.

Many of the known French Guiana's species, nonetheless, have never been observed during visual surveys to date. The main presumed causes are their rarity (or that of their host plants), low detectability (due to highly developed mimicry), poorly known biology (specific microhabitats), or inaccessibility (canopy, lianas, roots, epiphytes, or other substrates).

The taxa that remain particularly elusive during visual surveys include: *Sundarion*, *Stictopelta*, *Hemikyptha*, *Lallemandia nodosa*, *Centronodus*, *Paracentronodus*, *Ischnocentrus*, *Cymbormorpha*, *Eumela*, *Germariana*, *Alcmeone*, *Aspona*, *Allocyphotes*, *Cyphotes*, *Dectonura*, *Hebetica*, *Funkhouseriana*, *Hypheodana*, *Nasuconia*, *Atypa*, *Hyphinoe*, *Thrasymedes*, *Hygris*, *Smilidarnis*, *Thuris*, *Tumecauda*, and *Umbelligerus*. The vast majority of these taxa belong to the subfamily Darninae, which mostly comprises solitary species without ant associations.

Conversely, several genera and species are very rarely (or never) detected by light traps, with all observations resulting from visual surveys. These taxa include: *Cladonota*, *Scytodepsa exigua*, *Stictodepsa neotropicalis*, *Rhexia*, *Ochropepla*, *Umbonia*, *Eunusa concolor*, *Havilandia*, *Phyllotropis fasciata*, *Amblyophallus exaltatus*, *Dioclophara viridula*, and *Stegaspis fronditia*.

Host Plants (Table 1, Fig. 8)

We identified interactions with host plants belonging to 20 orders, 46 families, and 97 species.

The genus *Vismia* stands out as the most frequently observed host plant genus, with over 26 membracid species belonging to 20 genera and 4 subfamilies, primarily Smiliinae and Membracinae. These results are partly biased by the fact that *Vismia* species are very common along forest tracks, making them the most prospected plants.

Other taxa supporting relatively high membracid diversity include *Banara guianensis*, *Solanum rugosum*, *Solanum leucocarpon*, *Siparuna guianensis*, *Isertia coccinea*, *Miconia* spp., *Senna* spp., *Machaerium* spp., *Inga* spp., *Dalbergia* spp., *Trema micrantha*, and *Chromolaena odorata*. These plants host both generalist polyphagous membracids and apparently strict monophagous species.

Within the Aetalionidae, *Lophyraspis* species are most frequently found on Annonaceae, while other genera occur on diverse plant families and orders such as Lauraceae, Fabaceae, and Rubiaceae.

Microhabitats and Plant Phenology

Membracids most commonly position themselves at the tips of host plant stems, near meristems and growth zones. These are non-lignified parts where the bark is thinner and easier to pierce with the membracids' piercing-sucking mouthparts. A minority of species can feed by perforating directly into the



Figure 1.

A. *Notogonoides* nymphs and adults on *Ocotea splendens* (Lauraceae) with *Ectatomma tuberculatum* ants. **B.** *Anchistrotus* nymphs and *Ectatomma tuberculatum* ants. **C.** *Erechthia* aff. *bicolor* and *Cephalotes atratus* ants. **D.** *Erechthia nigrovittata* (nymph, male and female adults) and *Ectatomma tuberculatum* ant. **E.** *Biturritia capreolus* and *Cephalotes atratus* ants. **F.** *Phormophora maura* (nymphs and adults) and *Cephalotes atratus* ants.

lignified bark of branches; this is the case, for example, of *Heteronotus* and *Umbonia*, which are found on the branches of ice-cream beans (Fabaceae, *Inga* spp.). Others, such as *Cyphonia*, *Procyrtia*, and *Bolbonota*, sometimes feed on the main leaf veins, either on the upper or lower leaf surface.

The ontogenetic stage and phenology of the plant sometimes play an important role for membracids and can thus be fundamental to determine their presence. The stem bark must be sufficiently tender to be pierced by the rostrum of certain membracids. For many plants, this tenderness is found only on young shoots or on infructescences and inflorescences.

A pertinent example is *Erechtia diminuta*, which occurs on many Melastomataceae (*Miconia* spp.) but on *Miconia alata* only when it is flowering or fruiting (Fig. 2A), likely because *M. alata* stems are too woody and thick for this small species. Similar observations have been made for *Noranthea guianensis* (Marcgraviaceae), as well as *Pitcairnia cremersii* and *Catopsis berteroniana* (Bromeliaceae), which are occupied by membracids only during flowering periods, with insects positioning themselves on the floral stalks to feed and oviposit. Growing parts, infructescences, and inflorescences generally receive a higher sap flow from the plant, making these zones preferred sites for feeding or egg-laying, providing greater nutritional resources for the offspring.

In other species, fruits or their pedicels appear to be particularly targeted, as seen on *Aristolochia* (Aristolochiaceae), hosts of the very discreet *Hyphinoini*. This may be explained by the fact that *Aristolochia* are mostly woody lianas, which makes piercing by sap-sucking insects nearly impossible. Notably, some French Guianese *Aristolochia* species (*A. surinamensis* and *A. lepieurii*) have developed floral hood appendages resembling the dorsal abdominal spines of *Hyphinoe* larvae (Fig. 7A). We speculate that these *Aristolochia* species may have evolved a hood mimicking membracid nymphs to either give the impression of being already occupied by a larva—thus deterring other membracids seeking oviposition sites—or to attract membracid predators to eliminate any existing membracids. Alternatively, the membracids themselves may have evolved long dorsal spines during larval stages to better camouflage on the flower.

The infructescences of many plants, besides offering easily pierced zones, provide refuge areas that are difficult for predators to access. This is the case for *Solanum rugosum* and *Vismia*, where multiple membracid species sometimes aggregate within a specific zone at the heart of the fruit cluster.

Mono- and Polyphagy

The degree of polyphagy is highly variable among membracids, even within certain tribes or genera. For example, within the genera *Membracis* and *Enchenopa*, we find both polyphagous and monophagous species. Polyphagous species such as *Membracis foliatifasciata* and *Enchenopa concolor* occur on a wide diversity of plants across several families, whereas the monophagous species such as *Membracis foliata* and *Enchenopa* sp. “savanna,” are associated with a single genus or species of plant.

That said, we see four types of feeding specialisation: Strict Monophagy: Feeding on a single plant species. Broad Monophagy: Feeding on multiple plant species, but restricted to one or two closely related genera. Polyphagy: Feeding on several plant species within the same family, or within closely related families. Ultra-Polyphagy: Feeding on multiple plant species belonging to several different families and orders. Out of the total 315 species known from French Guiana, we did not evaluate 211 species, we consider Ultra Polyphagous 19 species, Polyphagous 15 species, Broad Monophagous 47 species and Strictly monophagous 23 species. Among the 104 species that we evaluated here, 21 have fewer than 3 data points, making their feeding regime difficult to assess reliably.

Within the genus *Lycoderes*, several monophagous species feed on Clusiaceae. The three species with pre-fracture lines—*Lycoderes brulei* (on *Clusia blattophylla* and *C. fockeana*), *Lycoderes elephantus* (on *Clusia panapanari*), and *Lycoderes carboneus* (on *Clusia palmicida*)—are generally positioned along the stem with their heads oriented toward the apex of the plant or sometimes on leaf margins. They camouflage well by mimicking burnt leaf fragments due to their coloration and complex shape. Speaking more broadly, we see associations of the *Notocera* and *Hypsoprora* genera with the Sapindaceae plant family; *Lophyraspis* with the Annonaceae plant family and *Cymbomorpha* along with most of Heteronotinae with the Fabaceae plant family.

Given that more than half of the membracid species of French Guiana have yet to be observed on their host plants and are collected only by passive capture methods (light or interception traps), it is difficult to reliably estimate the percentage of polyphagous versus monophagous species. Furthermore, some species have been observed only rarely, so our knowledge of the extent of their feeding range remains purely hypothetical.

Cultivated and Exotic Plants

In French Guiana, membracids rarely cause significant damage to the plants on which they feed, mainly because large-scale monocultures are uncommon. Nevertheless, some observations have shown that in large numbers, certain species can have detrimental effects on fruit trees and their production. This is the case for *Horiola* and *Anobilia* on cupuaçu and cacao trees (*Theobroma grandifolia* and *T. cacao*), and *Membracis*, particularly *M. foliatifasciata*, on soursop trees (*Annona squamosa*) and other Annonaceae. Both nymphs and adults congregate in large numbers on flower buds, young fruits, or their pedicels. The sap extraction is so intense that it causes fruit abortion. Boulard (1991) previously reported similar damage to soursop trees in Brazil caused by *Membracis suctifrutus*.

The pigeon pea (*Cajanus cajan*) serves as a substitute host plant for several species of the genera *Membracis*, *Enchenopa*, *Bolbonota*, and *Aurismastris*. Several membracid species have also been observed on the following cultivated exotic plants: cashew (*Anacardium occidentale*), ylang-ylang (*Cananga odorata*), breadfruit (*Artocarpus altilis*), and sea hibiscus (*Hibiscus tiliaceus*).

Overall, we speculate that membracids have a close association with pioneer and riparian vegetation. This may be due to the fact that these plants—found on rocky outcrops (e.g., *Clusia*) or in disturbed environments such as treefall gaps or forest edges (*Vismia*, *Banara*, *Goupia*, *Inga*, etc.)—grow more abundantly than species in dense, light-limited environments. Their generally faster growth and more frequent flowering results in a finer bark (when compared to understorey plants), which is more easily pierced by membracids. However, we emphasize that we sampled the most accessible microhabitats with high observation density, such as forest edges and treefall gaps, so our observations are biased. Surveys in dense understorey are time-consuming and yield limited results, while the canopy remains inaccessible. Nevertheless, the canopy may well host a large number of membracids.

Mutualistic Interactions Between Hymenoptera and Membracids (Table 2)

Over six years of observations, interactions between membracids and 26 species of Hymenoptera, belonging to 11 tribes and 2 families, have been recorded. Some observations remain unidentified, particularly sporadic interactions with Vespidae. It is very rare to observe multiple ant species interacting simultaneously with membracids (Fig. 2F); ants generally do not

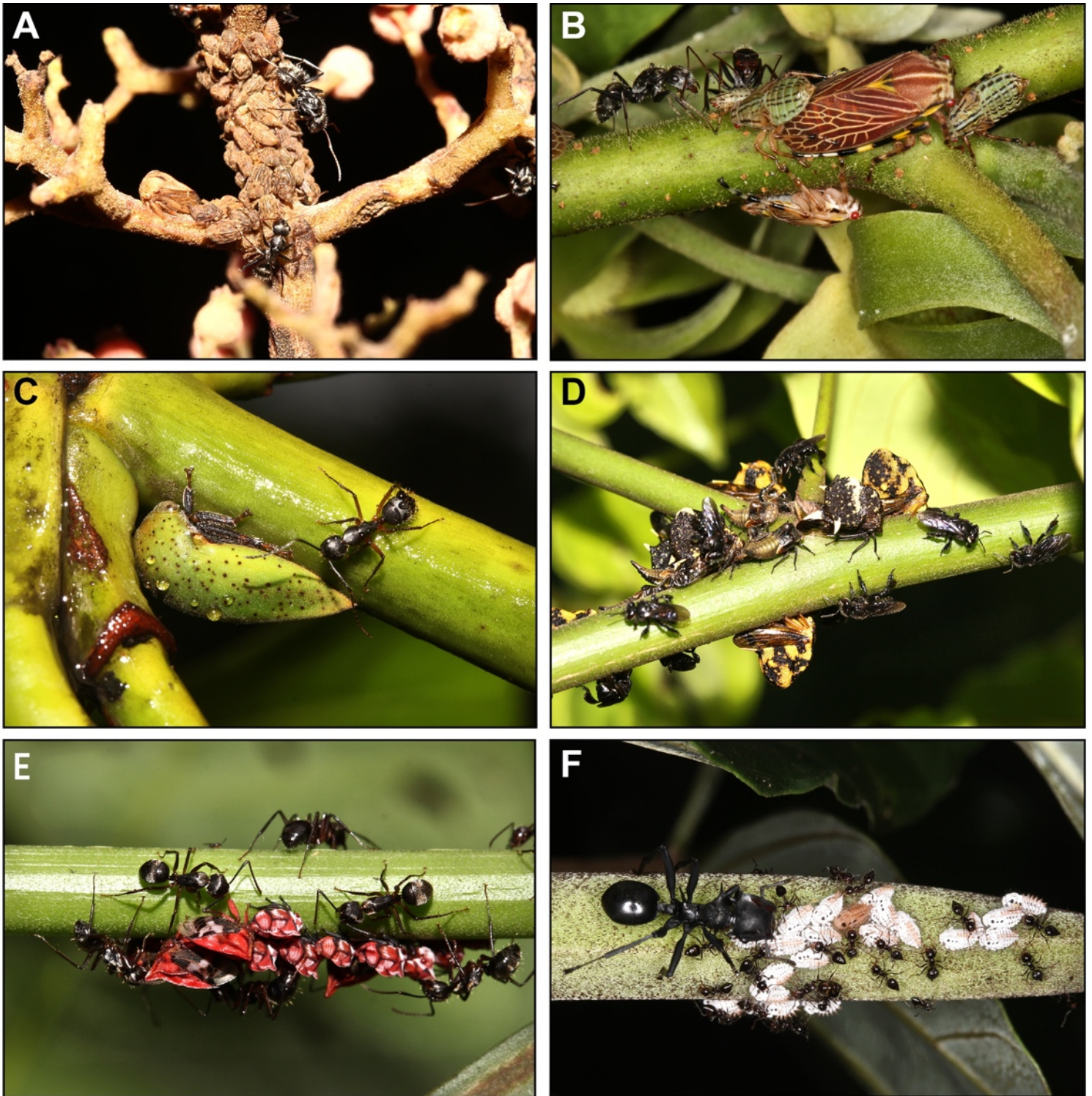


Figure 2.

A. *Erechtia diminuta*, nymphs and adult female, on inflorescence of *Miconia alata* (Melastomataceae) with *Camponotus* ants. **B.** *Aetalion reticulatum* and *Camponotus* cf. *novogranadensis* ant. **C.** *Darnis* on *Clusia* sp. and *Camponotus* ant. **D.** Membracid *Anchistrotus*, males, females, and larvae, interacting with *Meliponini* bees of the genus *Trigona*. **E.** *Tritropidia galeata*, nymphs and adults, and *Camponotus* ants. **F.** Very rare observation of several ant species observed simultaneously on the same group of membracids.

coexist in the same microhabitat, so multi-species associations are incidental and likely very rare.

According to observations, ants always arrive after the membracids. When membracids colonize a new plant, a female arrives by flight and lays eggs. Upon egg hatching, if arboreal ants are nearby, they usually detect the nymphs quickly and recognize the potential resources they provide. Membracid nymphs then become continuously surrounded by ants, whose numbers generally correlate with the size of the larval aggregation. These membracid-ant associations appear to be mutualistic, with no species showing strict dependence on a particular ant species. However, some associations seem more frequent, while others appear incompatible. For example, certain membracid species, such as *Guayaquila*, are consistently observed with the same ant species (Fig. 3C, 4E). This may reflect a shared preference for the same host plant or habitat rather than true incompatibility, which is unlikely. Again, observations are partly biased and too scarce for some species to confirm or refute hypotheses.

During all research conducted, only one instance was observed of an ant transporting a membracid larva: an *Ectatomma tuberculatum* ant carried a live nymph of *Anchistrotus*. This occurred within a group of ants and larvae. The ant transported the nymph from the apex of the plant to its base over several meters, after which it was no longer possible to follow. This atypical behavior remains unexplained; neither the nymph nor the ant showed any apparent abnormalities.

Degree of affinity of different tribes of Membracidae with ants (Table 3)

This simplified table provides a general trend for each tribe, without accounting for the significant disparities that sometimes exist within them. The Darninae, and more specifically the tribe Darnini, exhibit very low affinity for ants; observations of mutualistic interactions are rare and appear to be opportunistic (Fig. 2C). This is likely because most Darninae species are solitary, lay eggs sporadically, and their nymphs do not form gregarious aggregations. Consequently, ants have little incentive to remain near these larvae.

On *Chusia palmicida* occurs one of the largest “drop-shaped” Darnini. This Darnini consistently positions itself at the same location on the stem, just after a branch point, with its head oriented toward the base of the stem. Its camouflage is perfectly adapted—matching the green of the stem and positioned to mimic a stipule, although stipules are curiously absent in the Clusiaceae family. Its presence is often betrayed by ants gathered around a honeydew puddle on a leaf located directly beneath the larva. The membracid excretes honeydew through its anal tube, which falls by gravity onto the leaf below. Unlike other species, ants do not collect honeydew directly from the membracid’s abdomen tip but instead cluster around the honeydew puddle beneath.

In contrast to the Darnini, the Tragopini, which are predominantly gregarious species, show a strong affinity for ants, with mutualistic interactions being nearly ubiquitous. Between these two extremes—Darninae and Tragopini—other groups exhibit a wide range of affinities with ants. This variation sometimes shows no apparent correlation with tribal or generic affiliation, or even with gregariousness. Within the Aetalionidae, ant interactions are also very strong across all four genera recorded in French Guiana. *Ectatomma tuberculatum* (Fig. 1) is the ant species most frequently observed during surveys and has interactions with the greatest number of membracid species and genera.

Meliponine bees of the genus *Trigona* occasionally interact with membracids, particularly with nymphs of the genus *Anchistrotus* (Fig. 2D). These interactions resemble those with ants: *Trigona* bees collect honeydew excreted by larval anal tubes, and more rarely from adults.

Ant Shelters

Ant shelters (Fig. 5) are constructions made of soil or plant debris assembled by ants to provide additional protection to membracids. These shelters are built directly around larvae, on stems or under leaves, with entrances that allow only ants to pass. Three ant genera are known to construct such shelters: *Camponotus*, *Pheidole*, and *Azteca*. Shelter sizes vary, sometimes accommodating only one or two nymphs on the underside of a leaf, or several dozen membracids—adults and nymphs mixed—directly on the stem or trunk of the host plant. Shelters generally contain only a single membracid species. They are constructed on a wide diversity of plants, including Araceae, Fabaceae, and Melastomataceae.

Mimicry: Observations and Hypotheses (Table 4)

Membracid genera have been classified into five categories of mimicry based on the elements they appear to imitate or their defensive strategy: plant elements, excrement, ants or wasps, aposematic signaling, and undetermined. This classification is based solely on subjective reflections following observations (position, microhabitat, behavior, etc.) and proposes hypotheses due to the morphological resemblance of membracids to certain elements.

Vegetation mimicry

The majority of membracids appear to mimic plant elements (Fig. 7), which is easily explained by their sap-feeding habits and their frequent presence on stems or under leaves. The “drop-shaped” Darnini (genera such as *Alobia*, *Darnis*, *Stictopelta*, *Hebetica*, *Dectonura*) particularly mimic stipules, positioning themselves on stems often at branch axils, thereby perfecting their camouflage. Other elongated species, often with a frontal horn (e.g., *Enchenopa*, *Hemiptycha*), are generally found at leaf axils, also mimicking stipules.

Many membracid species are green and convex in shape, such as most *Cymbomorpha*, *Amastris*, *Eumela*, and *Germariana*, allowing them to blend into the photosynthetic parts of the plant. Smaller species, often brown or grayish, sometimes position themselves on the underside of leaves (*Tritopidia*, *Tropidoscyta*) or near dense fruit infructescences (*Aphetea*, *Dioclophara*), such as on *Vismia* and *Tapirira*. Some, with more complex shapes and often brown or yellow coloration, potentially mimic plant debris such as twigs or shriveled dry leaves (Fig. 6D) (*Lycoderides*, *Hypsoprora*, *Stegaspis*). The genus *Anchistrotus* likely mimics galls.

In brown hues and often with complex shapes, genera such as *Paracentronodus*, *Centronodus*, *Tolania*, *Tumecauda*, *Flexocentrus*, and *Smerdalea* resemble irregular bark covered with moss or lichen.

Mimicry of Excrement

The shapes of the genera *Aspona* and *Hypheodana* resemble bird droppings. The genus *Bolbonota* and other small Membracini appear to specifically mimic caterpillar frass.

Ant and Wasp Mimicry

Cyphonia, particularly *Cyphonia clavata*, mimics ants in a threatening posture. *Heteronotus nigrogiganteus* (synonym *Heteronotus formicoides*) mimics large ants. Members of the *Heteronotus spinosus* group, predominantly yellow with darker spots (Fig. 4B), mimic wasps (Vespidae).

Partial Ant Mimicry

Species of the tribe Tragopini have strong interactions with ants and mostly mimic the abdomen of the ant species they associate with (Fig. 3E). For example, the pronotum pattern of *Tropidolomia auriculata* resembles the abdominal coloration of certain *Camponotus* ants (Fig. 3F). Nymphs of some *Guayaquila* species share the same coloration as *Daceton armigerum*, with which they interact (Fig. 4E).

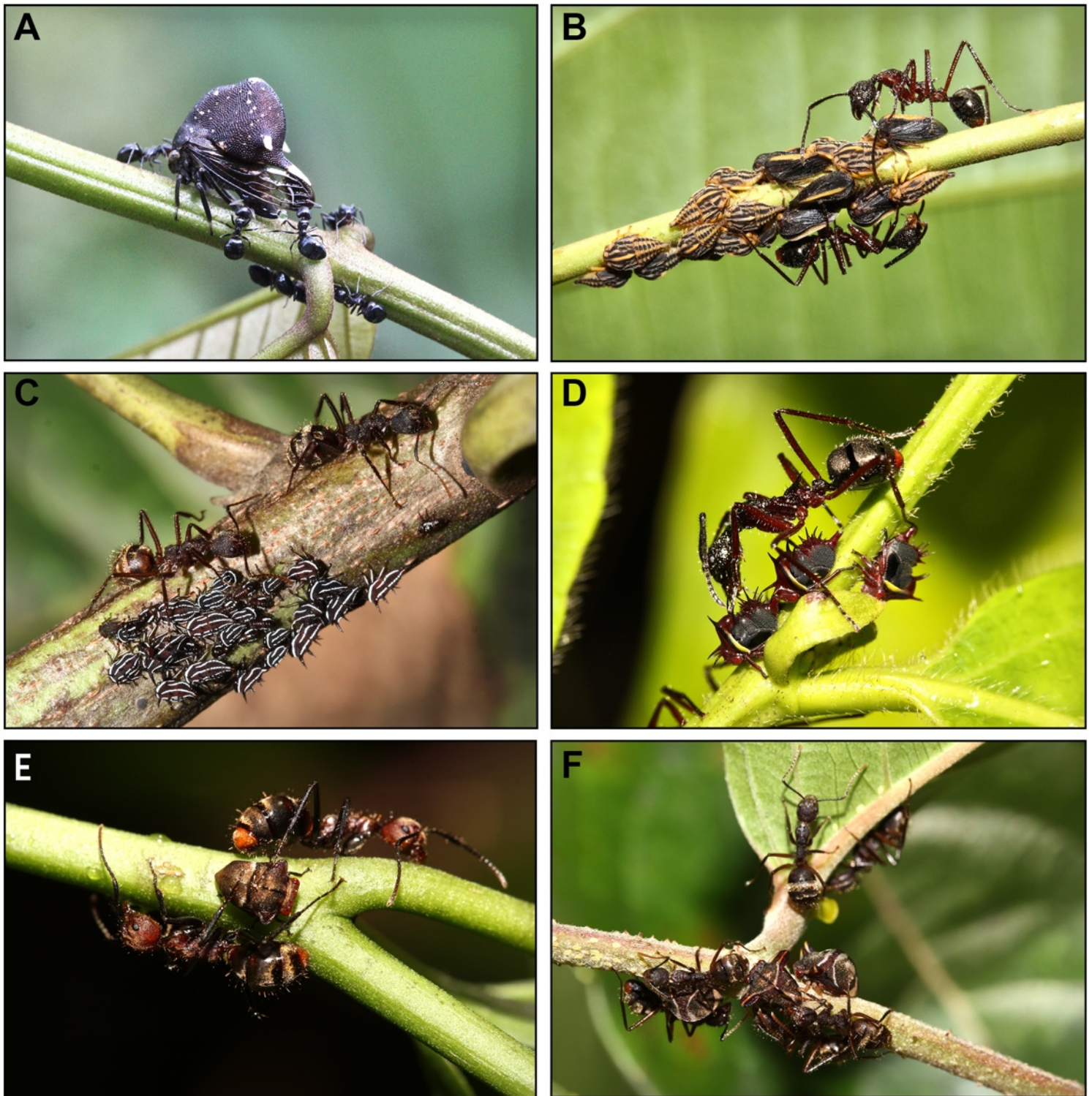


Figure 3.

A. *Anchistrotus* and *Dolichoderus debilis* ants. **B.** *Erechtia nigrovittata* and *Dolichoderus attelaboides* ants. **C.** *Guayaquila* nymphs and *Dolichoderus bidens* ants. **D.** *Neotynelia* nymphs and *Dolichoderus attelaboides* ants. **E.** *Tragopini* mimicking the abdomen of *Dolichoderus* ants. **F.** *Tropidolomia auriculata* and *Dolichoderus bidens* ants.

Aposematic Signaling

Several species exhibit alternating black and white patterns, and sometimes red and orange. This is observed in *Membracis*, *Enchophyllum*, *Folicarina*, *Smilidarnis*, *Phyllotropis*, and some *Darnis*, *Harmonides*, *Chelyoidea* (Fig. 4F), or *Tritropidia*. Some larvae, such as those of *Notogonioides*, are entirely red, potentially serving as aposematic signals. These nymphs strongly resemble certain entirely red *Thysanoptera* species. Some nymphs of *Neotynelia* display red, yellow, and black coloration.

If the bright coloration of these species indeed functions as aposematic signalling, it likely serves to deter vertebrate predators. This hypothesis is supported by the absence, to our knowledge, of any reported deterrent effect of aposematic insects against predation by other invertebrates.

Undetermined Mimicry

While mimicry is evident for many membracids, for others it remains an enigma, opening the door to numerous hypotheses. In most cases, understanding what is mimicked is easier when observing species in their natural habitat, on a particular host plant, or exhibiting specific behaviors that enhance their mimicry. A pertinent example is *Stylocentrus ancora*, whose mimicry was unclear until observed in situ on its host plant, *Scleria secans*. Adults position themselves on the underside of long leaves or near fruits that they closely resemble (Fig. 6E). Another example is *Heteronotus*, which, in addition to mimicking wasps (Vespidae), exhibits rapid flight and jerky movements very similar to many wasps.

Lallemandia nodosa, despite being highly detectable on **light trap** and present at nearly all surveyed sites, has never been observed on its host plant. It appears to mimic a fly.

Most *Hypsoprurini* (*Hypsoprora*, *Cladonota*, *Notocera*) are covered with a whitish waxy substance and elongated outgrowths that may resemble entomopathogenic fungi of the *Cordyceps* group. We hypothesize that invertebrate predators may avoid consuming insects potentially infected by entomopathogenic fungi to prevent contracting the fungus themselves. According to our observations, insects infected by fungi are not consumed by other invertebrates in the forest.

The genera *Funkhouseriana*, *Nasuconia*, and *Chelyoidea* resemble certain beetles of the families Chrysomelidae or Curculionidae.

Comparative morphology of pronotum helmets (Table 5)

Table 5 roughly groups genera into several morphological categories based on the ornamentation of the pronotum helmet, primarily considering the number and arrangement of spiny projections. Since helmet shape can vary considerably within a single genus (Sugiura et al. 2025), the form most representative of the species found in French Guiana was used for classification.

Posterior Projection Developed into a Spine

Twenty-three genera are classified within this category, which is the most widespread. All genera classified as “drop-shaped” Darnini according to Roy (2007) belong to this category. Other genera in this category belong to several subfamilies: Heteronotinae, Smiliinae, Centrotinae, Membracinae, and Darninae. This distribution demonstrates strong evolutionary convergence towards this morphology, which serves both mimetic and defensive functions. In most cases, the helmet covers the entire abdomen and sometimes part of the wings, ending in a more or less acute spine. The most striking case of evolutionary convergence is the genus *Hygris* (Smiliinae) and the “drop-shaped” Darninae genera: *Stictopelta*, *Alobia*, *Darnis*, *Hebetica*, *Dectonura*. All have a drop-shaped dorsal profile and mimic a greenish stipule.

Anterior Horn and Posterior Projection

This category mainly includes genera of the subfamily Membracinae (*Aconophora*, *Guayaquila*, *Potnia*, *Umbonia*, *Enchenopa*, *Enchophyllum*, *Phylia*) and some representatives of Smiliinae (*Notogonioides*, *Hemiptycha*).

We note that the “anterior horn” morphology is always accompanied by the “posterior projection” morphology, suggesting that the posterior projection, common to all Smiliinae and Membracinae, is an older character than the appearance of anterior projections. Furthermore, in several mostly projectionless genera (*Havilandia*, *Tritropidia*, *Talipes*), some species are beginning to develop frontal protuberances.

Two Supra-Humeral Horns

This morph, corresponding to the “bicorn” group of Roy (2007), includes genera from nearly all subfamilies: Heteronotinae, Centronodinae, Smiliinae, Stegaspidinae, Darninae, Membracinae. In most genera, the supra-humeral horns are robust, with a broad base and pointed tip, and the posterior projection is also acute. This morphological pattern has appeared in almost all subfamilies, likely due to its high effectiveness in reducing predation. Most of these projections appear to play important roles both in mimicry and mechanical defense, particularly the spines. In this category, only the genus *Tolania* (Nicominae) lacks a posterior projection. Only the Tragopini genera (*Todea* and *Tropidolomia*) have a posterior projection that is not acute and covers almost the entire wings. In other genera, the wings are fully exposed but the helmet ends in a spine that runs along the upper wing margin.

Complex Multi-Spined Projection

Three subfamilies are represented in this category: Smiliinae by the genus *Cyphonia*, Heteronotinae by *Heteronotus*, and Stegaspidinae by *Stylocentrus*, *Bocydium*, *Smerdalea*, and *Umbelligerus*. Species of *Heteronotus* exhibit complex and varied projections: supra-humeral horns are long, thin, and curved in *Heteronotus albospinosus*, while short, broad, and straight in *Heteronotus nigrogiganteus*. The posterior projection ends in a nodule typically bearing three spines. The *Heteronotus delineatus* group has reduced or absent supra-humeral horns in males and a very long, thin posterior projection ending in a nodule.

The Pre-Fracture Line

The pre-fracture line is a circular zone of weakened cuticle located at the base of the helmet. As a result, the helmet detaches from the membracid's body at this point when pressure is applied, allowing the membracide to escape the predator. This defense mechanism is detailed by Boulard (1983). Only two genera, belonging to different subfamilies, exhibit this feature: *Anchistrotus* (Heteronotinae) and *Lycoderides* (Stegapidae). All *Anchistrotus* species possess this mechanism, while only the four species of the *brulei* group within *Lycoderides* have it. Other genera lack this pre-fracture line but have a thin helmet with a weak point that breaks easily (*Bocydium*, *Stylocentrus*, *Heteronotus*, *Cladonota*). It should be noted that individuals with broken helmets show no behavioural changes, even in gregarious species. It is also assumed that this does not affect their ability to reproduce, as cases of mating with one of the mutilated specimens have already been observed in *Cyphonia clavata*.

Predation

The evolution of the great diversity of mimicry strategies in membracids may be due to strong predation pressure. Different cases of predation observed in the field are discussed here.

Opportunistic or Generalist Predation

Salticidae (jumping spiders) appear to be the primary generalist predators of membracids, preying on both nymphs and adults, even on large species such as *Heteronotus*. Like all insects, membracids are also sometimes caught in generalist spider webs. Several

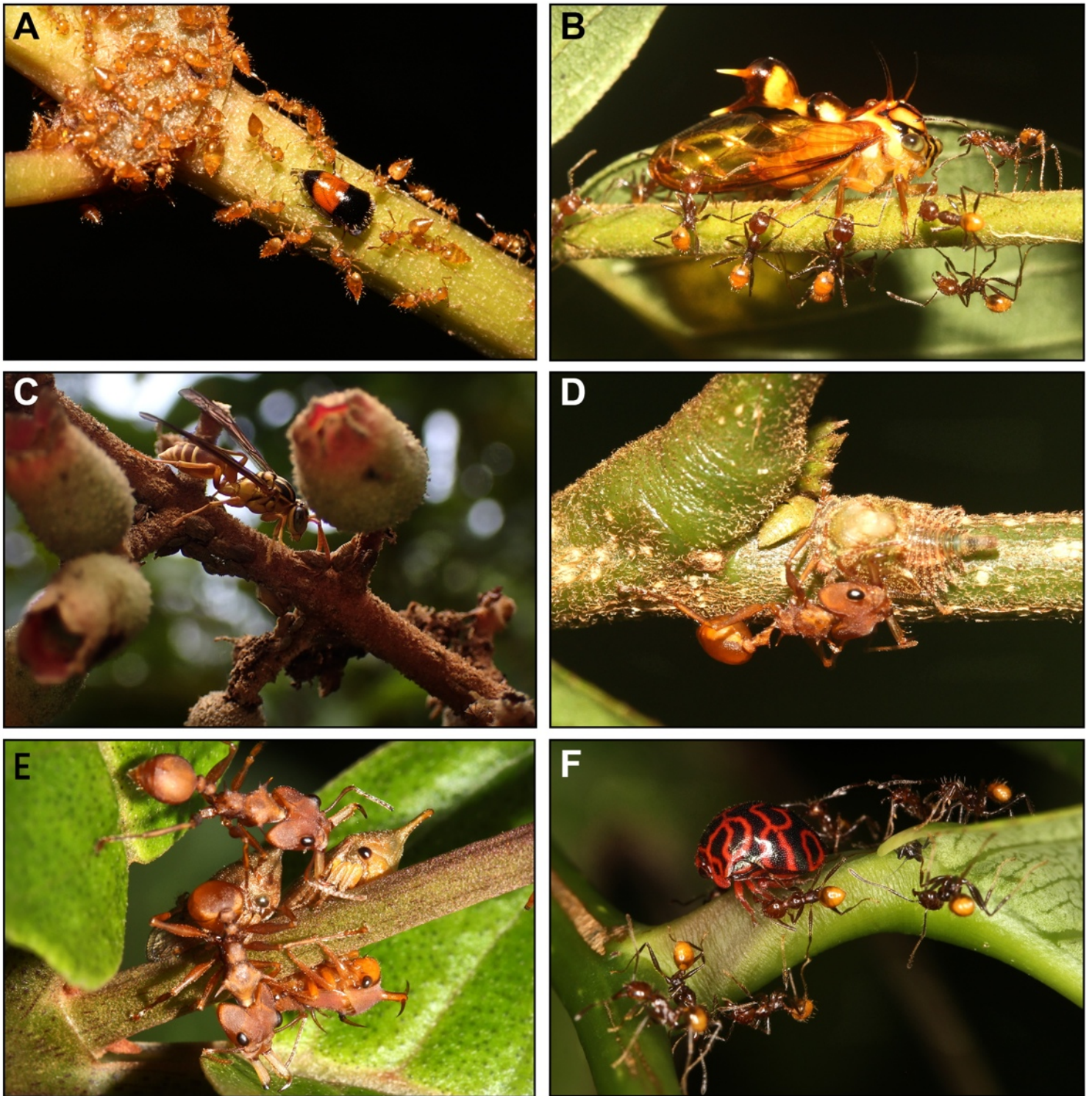


Figure 4.

A. *Harmonides dispar* and *Crematogaster* ants. **B.** *Heteronotus spinosus* and *Pheidole* ants. **C.** Interaction of a wasp with *Erechtia diminuta*. **D.** *Heteronotus* nymph and *Daceton armigerum* ant. **E.** *Guayaquila* nymphs and *Daceton armigerum* ants. **F.** *Tragopa* (*Chelyoidea*) *annulata* and *Pheidole* sp. ants.

observations of predation by Reduviidae (assassin bugs) have also been made on nymphs or adults of *Cyphonia clavata* or *Enchenopa*. Less frequently, predation by various generalist insects such as Anisoptera (dragonflies), Mantodea (mantises), *Paraponera* (bullet ants), and Thomisidae (crab spiders) has been observed. Occasionally, adult membracids are found infected by *Cordyceps* entomopathogenic fungi. It is also common to observe parasitic mites on adults of many species. No observations of predation on membracids by vertebrates have been made, likely because vertebrates are highly sensitive to human presence, making such observations difficult without a hide in optimal conditions. Monitoring membracids using macro photo-traps could provide interesting insights into behaviour, mutualistic interactions and cases of predation, whether by specialist parasitoids, other insects or small vertebrates. Recent technological advances in data acquisition and analysis tools could enable us to provide answers to many of our hypotheses (Darras K., Balle M., Xu W. et al., 2024).

Specialized Predation

The specialized micro-hymenopterans parasitoid primarily target eggs or larval stages. Some observations have shown parasitoid hymenopterans waiting for extended periods near female membracids guarding their eggs or the nymphs tended by ants, awaiting for an opportunity to deposit their own eggs. Parasitoid oviposition is difficult to observe due to their small size, and tracking development is even more complex. In French Guiana, no in-depth investigation has yet been conducted on this topic to establish the degree of specialization in predation, the strategies deployed, and larval development cycle durations.

As reported by Jacobi (2008) in Costa Rica and Callan (1977) in Trinidad, certain hymenopterans of the genus *Hoplisoides* (Crabronidae) specialize in predation on adult membracids of the genus *Umbonia*. Similar observations have been on *Umbonia spinosa* in French Guiana made. The different stages of this predation are detailed below.

Note on *Hoplisoides* Predation on *Umbonia spinosa* (Fig. 6F)

First, the wasp *Hoplisoides* digs a burrow in dry loamy soil. The hymenopteran digs using its front legs and projects the excavated sand backward between its two hind pairs of legs. It may encounter larger gravel, up to the size of its head; in this case, the hymenopteran grasps it with its mandibles and drags it to the outside of the burrow. If the gravel is too large to be excavated, it bypasses it by digging in another direction; if this is impossible, it abandons the burrow and digs another. It may spend 10 to 30 minutes digging its burrow. Afterward, it flies off and quickly returns with prey, always the same: an adult *Umbonia spinosa*. The flight of a *Hoplisoides* carrying its prey is noisy and linear, reflecting the effort expended by the hymenopteran. *Hoplisoides* carrying male *Umbonia*, which are much lighter, fly more easily and produce less noise. The hymenopteran always holds its prey in the same way, venter to venter; the membracid is completely paralyzed and does not move at all. It is held at the base of the wings, with the wasp using its middle legs for this purpose, and once on the ground, it uses its hind legs to walk and its forelegs to dig. The membracid is dragged into the nest, approximately one centimeter in diameter and several centimeters deep, headfirst. The hymenopteran then completely seals the gallery with fine sand in a few minutes and proceeds to search for another area to dig a new gallery. It has not been possible to determine at what point the hymenopteran's egg (presumably a single egg) is laid on the membracid, where it is laid, or the duration of the cycle. Numerous *Hoplisoides* individuals may occupy a restricted space of a few square meters, and the same site is sometimes used for several years, provided it meets at least the following two conditions: the presence of *Umbonia spinosa* and soil suitable for burrow excavation.

Conclusion

Although this article presents numerous novel ecological observations concerning the family Membracidae in French Guiana, much remains to be discovered. Many species, and even several genera, have yet to be observed in their natural habitat; as a result, the morphology of their larval stages, their development cycle, their host plants, and their ecology remain completely unknown. This clearly shows the scope of discovery remaining for this family in this territory. These lists of interactions and tables of comparative morphology are only starting points for more advanced research on specific topics such as evolutionary convergences, comparative biogeography with host plants on a larger scale, possible co-evolution with mutualistic hymenopteran species, and many others. Numerous hypotheses raised here remain to be validated or refuted. This data will also be a valuable resource for anyone wishing to observe them, rear them, or conduct research to learn more about them.

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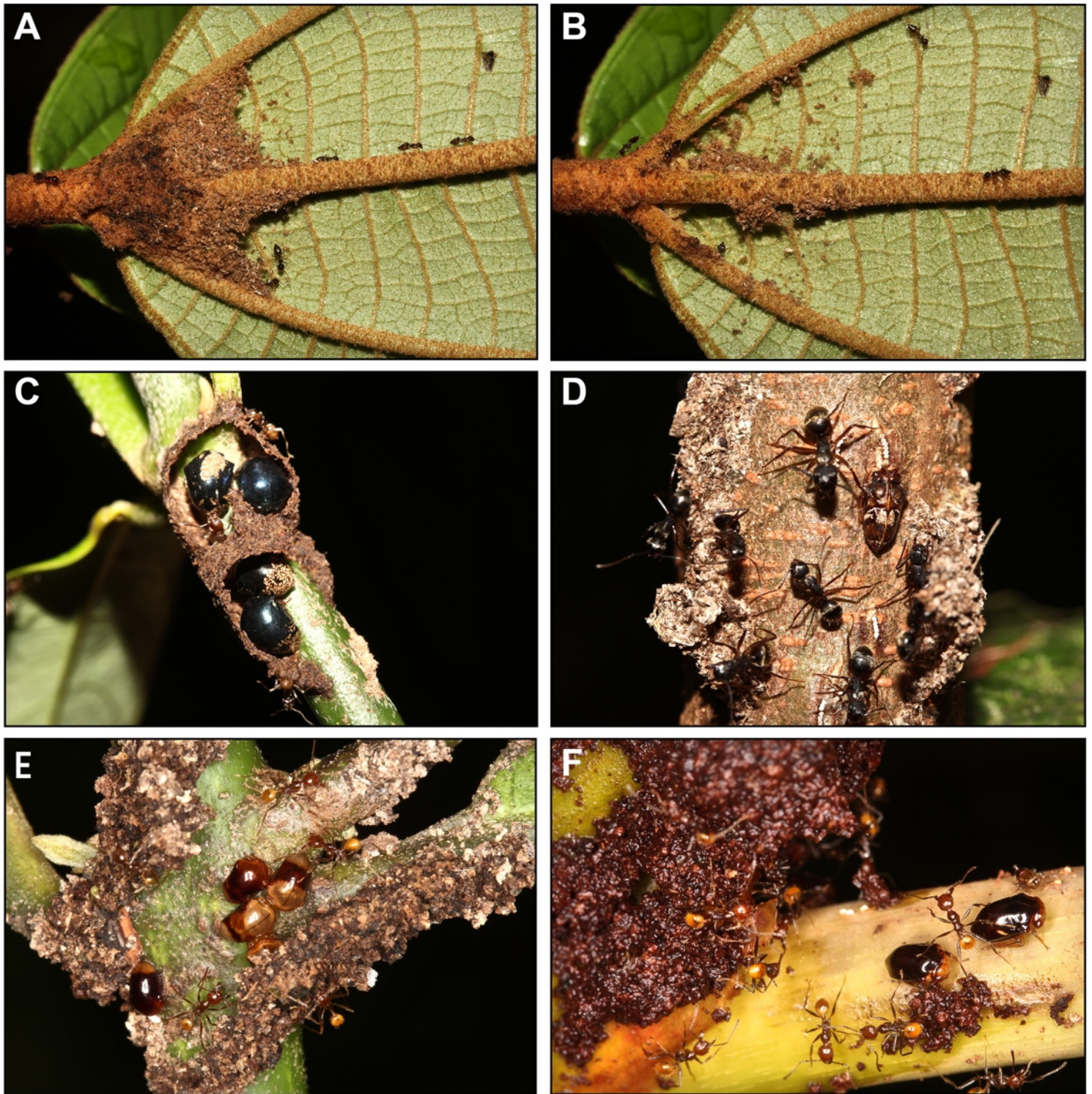


Figure 5.

A. *Crematogaster* ant shelter on the underside of a Melastomataceae leaf. B. Interior of the same shelter, showing two membracid larvae. C. *Chelyoidea* inside an *Azteca* ant shelter. D. *Tragopa corniculata* and eggs within a *Camponotus* ant shelter. E. Tragopini inside a *Pheidole* ant shelter. F. Tragopini on Araceae, inside a *Pheidole* ant shelter.

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Correspondence with the editor. – JL

Manuscript writing. – JL & GS

Manuscript traduction. – GS

Manuscript proofreading. – JL, GS & EC

Bibliographic research. – JL & GS

Fieldwork. – JL & EC

Identification of Membracidae. – JL

Botanical identification. – GS & JL

Authors of the figures. – JL

¹ JL = Lapèze J. – GS = Sellan G. – EC = Cocchi E.

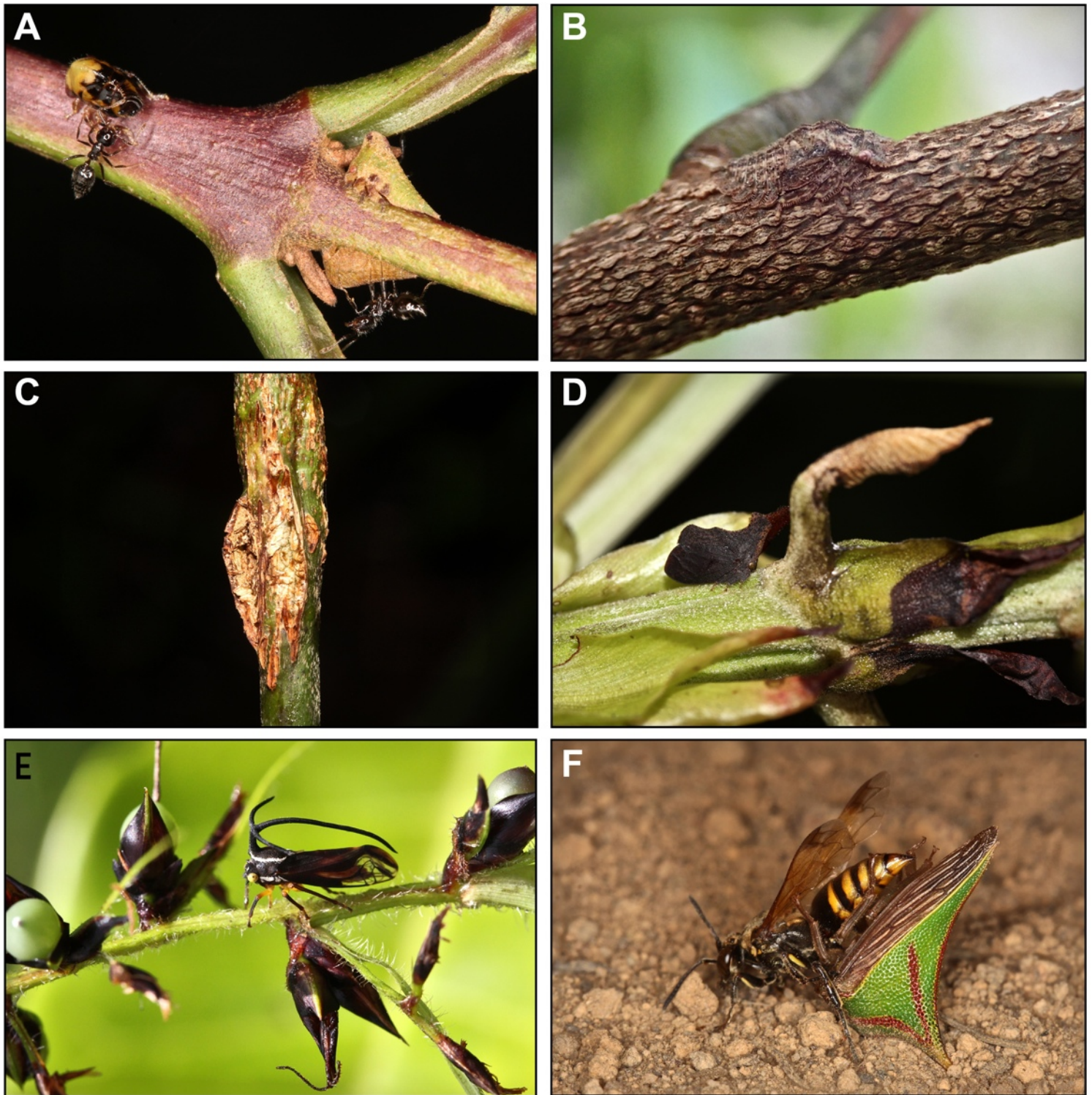


Figure 6.

A. Nymphs of *Lycoderides* and *Amastris* on *Vismia* sp. **B.** nymphs of *Nicomia* on a Fabaceae species. **C.** Lesion on the stem of a liana following oviposition by a membracid of the genus *Potnia*. **D.** *Stegaspis fronditia*, female, on *Isertia coccinea*. **E.** *Stylocentrus ancora* amidst the infructescences of *Scleria secans*. **F.** *Umbonia spinosa* preyed upon by *Hoplisoides* (Crabronidae).

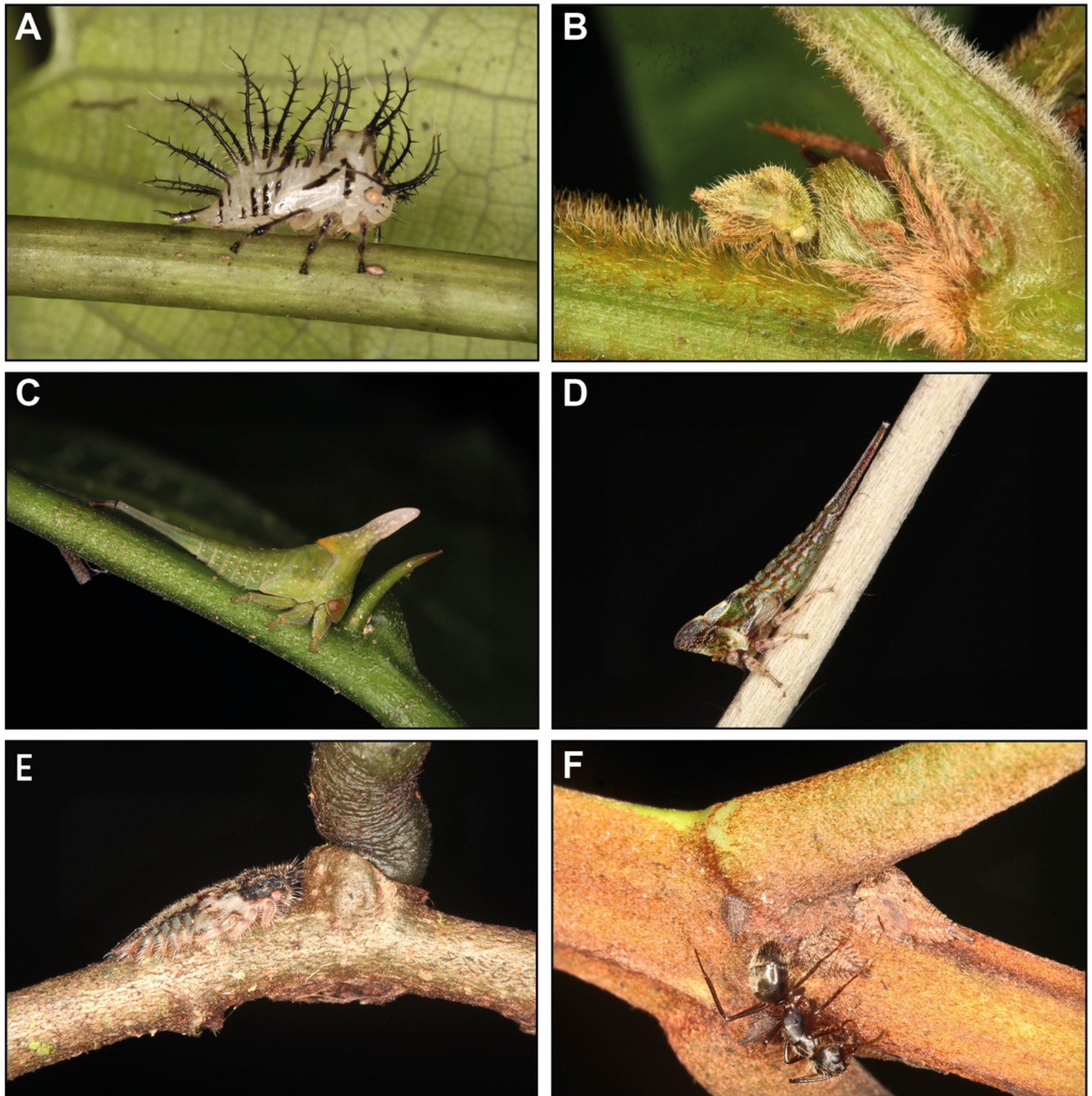


Figure 7.

A. *Hyphinoe* nymph on *Aristolochia* sp. liana. **B.** *Rhexia* nymph on *Paullinia rubiginosa*. **C.** *Stictopelta* nymph on *Celtis iguanea*. **D.** *Tolanina* nymph on *Sabicea* sp. **E.** Undetermined nymph on “liane tortue” (*Bauhinia* sp.). **F.** *Procyrtia* nymph on *Byrsonima* cf. *aerugo*.

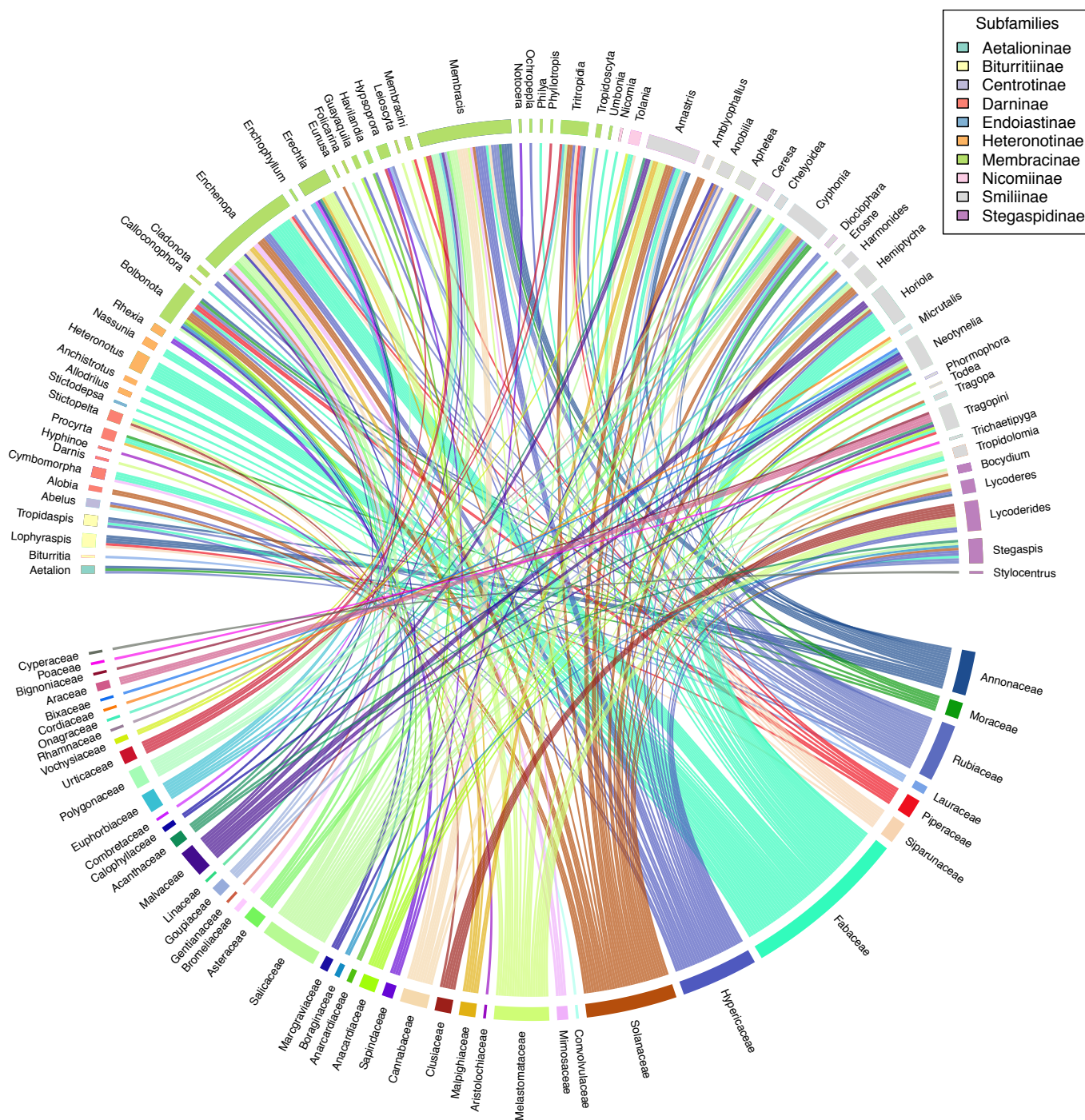


Figure 8.

Circos plot showing the feeding preference of Membracidae and Aetalionidae genera (labels on the upper part of the figure) for several plant families (labels on the lower part of the figure). Chords represent the interactions between genera and plant families, with each subfamily of Membracidae color-coded and shown in the legend.

Résumé

Lapèze J., Sellan G. & Cocchi E., 2025. – Synthèse des connaissances sur les membracides et les aetalions de Guyane française (Hemiptera : Auchenorrhyncha : Membracidae, Aetalionidae). Partie II : biologie, plantes-hôtes et interactions écologiques. *Faunitaxys*, 13(39) : 1 – 25.

Cet article fait état des connaissances des plantes hôtes et des interactions mutualistes des membracides de Guyane suite à six années de prospection sur ce territoire entre 2016 et 2023. De brèves notes sont présentées concernant les micro-habitats, la phénologie, le polyphagisme, la prédation et le parasitisme. Quelques hypothèses sont proposées pour expliquer des convergences évolutives ou des mécanismes de défense. Une approche de classification des membracides selon des traits écologiques (degré d'affinités avec les fourmis) ou morphologiques (mimétisme, forme des casques) est également présentée.

Mots-clés. – Hemiptera, Auchenorrhyncha, Membracidae, Aetalionidae, Formicidae, mimétisme, polyphagie, mutualisme, morphologie, prédation, Guyane française.

Table 1. Host plants and associated Membracids

Species for which nymphs or egg clutches have been observed on the host plant are indicated in **bold**. This distinction separates “primary” host plants, where reproduction has been confirmed, from “secondary” host plants, where reproduction has not been observed but the presence of feeding adults has been recorded.

Host plant			Membracidae / Aetalionidae
Order	Family	Genus or species	Genus or species
Alismanthales	Araceae	<i>Philodendron billietiae</i>	Tragopini
Alismanthales	Araceae	<i>Philodendron duckei</i>	Tragopini
Alismanthales	Araceae	<i>Philodendron placidum</i>	Tragopini
Asterales	Asteraceae	<i>Chromolaena odorata</i>	<i>Enchenopa albidorsa</i>, <i>Enchenopa squamigera</i>, <i>Cyphonia clavata</i>, <i>Cyphonia trifida</i>, <i>Membracis tectigera</i>, <i>Ceresa</i>
Boraginales	Boraginaceae	/	<i>Stegaspis fronditia</i> , <i>Bolbonota aspidistrae</i> ,
Boraginales	Cordiaceae	<i>Varronia</i> sp.	<i>Microtalis</i>
Caryophyllales	Polygonaceae	/	<i>Folicarina bicolor</i>
Caryophyllales	Polygonaceae	<i>Coccoloba</i> sp.	<i>Membracis foliatafusca</i>, <i>Aphetea</i>
Caryophyllales	Polygonaceae	<i>Coccoloba</i> cf. <i>lucidula</i>	Chelyoidea
Caryophyllales	Polygonaceae	<i>Coccoloba latifolia</i>	<i>Membracis foliata</i>
Caryophyllales	Polygonaceae	<i>Coccoloba lucidula</i>	Chelyoidea
Caryophyllales	Polygonaceae	<i>Coccoloba mollis</i>	<i>Membracis foliata</i>
Ericales	Marcgraviaceae	<i>Norantea guianensis</i>	<i>Bolbonota</i>, <i>Enchenopa concolor</i>, <i>Anobilia</i>
Fabales	Fabaceae	<i>Abarema jupunba</i>	<i>Heteronotus</i> cf. <i>delineatus</i>
Fabales	Fabaceae	<i>Cajanus cajan</i>	<i>Enchenopa gracilis</i>, <i>Bolbonota</i>
Fabales	Fabaceae	<i>Dalbergia</i> sp.	<i>Anchistrotus</i>, <i>Enchenopa squamigera</i>, <i>Aphetea</i>, <i>Nicomia</i>, <i>Horiola</i>, <i>Stegaspis fronditia</i>, <i>Cyphonia clavata</i>, <i>Enchenopa gracilis</i>, <i>Cymbomorpha</i>, <i>Nassunia</i>,

Fabales	Fabaceae	<i>Eperua</i> sp.	<i>Enchenopa concolor</i> , <i>Neotynelia</i> , <i>Horiola</i> , <i>Tolania</i>
Fabales	Fabaceae	<i>Inga</i> sp.	<i>Cymbomorpha</i> , <i>Tragopa corniculata</i> , <i>Tragopini</i> , <i>Tropidaspis</i> , <i>Heteronotus spinosus</i> , <i>Procyrtia</i> ,
Fabales	Fabaceae	<i>Inga</i> cf. <i>melinonis</i>	<i>Heteronotus spinosus</i>
Fabales	Fabaceae	<i>Inga splendens</i>	<i>Heteronotus horridus</i> , <i>Umbonia spinosa</i>
Fabales	Fabaceae	<i>Inga stipularis</i>	<i>Allodrilus</i> , <i>Tolania</i>
Fabales	Fabaceae	<i>Machaerium</i> sp.	<i>Enchenopa concolor</i> , <i>Anchistrotus</i> , <i>Rhexia</i> , <i>Allodrilus</i> , <i>Amastria</i> , <i>Horiola</i> , <i>Tropidolomia auriculata</i> , <i>Nassunia</i> , <i>Heteronotus</i>
Fabales	Fabaceae	<i>Macherium</i> cf. <i>polyphyllum</i>	<i>Nassunia</i>
Fabales	Fabaceae	<i>Parkia</i> sp.	<i>Horiola</i>
Fabales	Fabaceae	<i>Pterocarpus</i> cf. <i>rhorii</i>	<i>Cymbomorpha vaginata</i>
Fabales	Fabaceae	<i>Pterocarpus officinalis</i>	<i>Calloconophora</i> , <i>Enchenopa concolor</i> , <i>Horiola</i> , <i>Procyrtia</i>
Fabales	Fabaceae	<i>Recordoxylon speciosum</i>	<i>Heteronotus</i>
Fabales	Fabaceae	<i>Senegalia tenuifolia</i>	<i>Philya pallidipennis</i>
Fabales	Fabaceae	<i>Senna</i> sp.	<i>Tropidolomia</i> , <i>Aphetea</i> , <i>Horiola</i> , <i>Amastria</i> , <i>Erosne</i>
Fabales	Fabaceae	<i>Senna chrysocarpa</i>	<i>Stictopelta</i>
Fabales	Fabaceae	<i>Senna multijuga</i>	<i>Enchenopa concolor</i> , <i>Enchenopa squamigera</i> , <i>Heteronotus</i> , <i>Membracis</i>
Fabales	Fabaceae	<i>Swartzia panacoco</i>	<i>Horiola picta</i> , <i>Enchenopa squamigera</i>
Fabales	Fabaceae	<i>Tachigali</i> sp.	<i>Horiola</i> , <i>Stictodepsa</i>
Gentianales	Gentianaceae	<i>Chelonanthus</i>	<i>Enchenopa</i>
Gentianales	Rubiaceae	<i>Isertia coccinea</i>	<i>Membracis tectigera</i> , <i>Membracis lefebvrei</i> , <i>Aetalion reticulatum</i> , <i>Tritropidia</i> , <i>Dioclophara viridula</i> , <i>Anobilia</i> , <i>Bolbonota</i> , <i>Hemiptycha cultrata</i> , <i>Stegaspis fronditia</i> , <i>Membracis nigra</i> , <i>Cyphonia clavata</i> , <i>Enchenopa squamigera</i> , <i>Hypsoprora bifida</i>
Gentianales	Rubiaceae	<i>Isertia spiciformis</i>	<i>Tropidaspis</i> , <i>Erechtia gibbosa</i> , <i>Tropidoscyta</i>

Gentianales	Rubiaceae	<i>Sabicea cinerea</i>	<i>Cladonota foliata</i> , <i>Stegaspis fronditia</i> , <i>Ceresa</i>
Gentianales	Rubiaceae	<i>Uncaria</i> sp.	<i>Harmonides reticulata</i> , <i>Enchophyllum markantum</i>
Lamiales	Acanthaceae	<i>Mendoncia hoffmannseggiana</i>	<i>Erechtia</i>
Lamiales	Acanthaceae	<i>Polylychnis fulgens</i>	<i>Stegaspis fronditia</i> , <i>Tragopini</i> , <i>Amastris</i>
Lamiales	Bignoniaceae	<i>Fridericia patellifera</i>	Tragopini
Laurales	Hernandiaceae	<i>Sparattanthelium wonotoboense</i>	<i>Tolania</i>
Laurales	Lauraceae	<i>Cassytha filiformis</i>	<i>Hypsoprora expansa</i>
Laurales	Lauraceae	<i>Ocotea guianensis</i>	<i>Amastris</i>
Laurales	Lauraceae	<i>Rhodostemonodaphne grandis</i>	<i>Biturritia capreolus</i>
Laurales	Siparunaceae	<i>Siparuna guianensis</i>	<i>Lophyraspis</i> , <i>Amastris</i> , <i>Anobilia</i> , <i>Tolania</i> , <i>Membracis tectigera</i> , <i>Ceresa</i> , <i>Tritropidia</i> , <i>Enchenopa albidorsa</i>
Magnoliales	Annonaceae	/	<i>Amastris angulata</i> , <i>Amastris subangulata</i> , <i>Tritropidia</i> , <i>Bolbonota</i> , <i>Membracis tectigera</i> , <i>Ceresa</i>
Magnoliales	Annonaceae	<i>Anaxagorea</i> cf. <i>dolichocarpa</i>	<i>Lycoderes fabricii</i>
Magnoliales	Annonaceae	<i>Annona</i> sp.	<i>Lophyraspis</i>
Magnoliales	Annonaceae	<i>Annona muricata</i>	<i>Neotynelia</i> , <i>Tropidaspis</i> , <i>Membracis foliatifasciata</i>
Magnoliales	Annonaceae	<i>Annona squamosa</i>	<i>Aetalion reticulatum</i>
Magnoliales	Annonaceae	<i>Cananga odorata</i>	<i>Lophyraspis muscaria</i> , <i>Membracis foliatifasciata</i> , <i>Membracis tectigera</i>
Magnoliales	Annonaceae	<i>Guatteria</i> sp.	<i>Lophyraspis spinosa</i>
Malpighiales	Calophyllaceae	<i>Mahurea palustris</i>	<i>Erechtia</i> , <i>Neotynelia</i>
Malpighiales	Clusiaceae	<i>Clusia blattophila</i>	<i>Lycoderides brulei</i>
Malpighiales	Clusiaceae	<i>Clusia fockeana</i>	<i>Lycoderides brulei</i>
Malpighiales	Clusiaceae	<i>Clusia palmicida</i>	<i>Lycoderides carboneus</i> , <i>Stictopelta squara</i>

Malpighiales	Clusiaceae	<i>Clusia panapanari</i>	<i>Lycoderides elephantus</i> , <i>Lycoderides brulei</i>
Malpighiales	Euphorbiaceae	<i>Acalypha diversifolia</i>	<i>Membracis nigra</i> , <i>Erechtia cristalta</i>
Malpighiales	Euphorbiaceae	<i>Aparisthmium cordatum</i>	<i>Neotynelia vertebralis</i> , <i>Tritropidia nimbata</i> , <i>Hemiptycha obtecta</i>
Malpighiales	Euphorbiaceae	<i>Dalechampia</i>	<i>Cyphonia clavata</i>
Malpighiales	Euphorbiaceae	<i>Sagotia racemosa</i>	<i>Erechtia cristalta</i>
Malpighiales	Goupiaceae	<i>Goupia glabra</i>	<i>Neotynelia</i> , <i>Membracis foliatafasciata</i> , <i>Cyphonia clavata</i> , <i>Enchenopa squamigera</i>
Malpighiales	Hypericaceae	<i>Vismia</i> sp.	<i>Havilandia pruinosa</i> , <i>Dioclophara viridula</i> , <i>Cladonota grisea</i> , <i>Amastris</i> , <i>Lycoderes fabricii</i> , <i>Bolbonota</i> , <i>Ochropepla</i> , <i>Stegaspis fronditia</i> , <i>Membracis nigra</i> , <i>Neotynelia pubescens</i> , <i>Guayaquila</i> , <i>Tritropidia</i> , <i>Membracis tectigera</i> , <i>Enchenopa albidorsa</i> , <i>Enchenopa concolor</i> , <i>Aphetea</i> , <i>Tropidaspis</i> , <i>Anobilia</i> , <i>Harmonides reticulata</i> , <i>Membracis foliatafasciata</i> , <i>Enchenopa gracilis</i> , <i>Horiola picta</i> , <i>Abelus luctuosus</i> , <i>Lycoderides</i> , <i>Cyphonia clavata</i> , <i>Membracis dorsata</i> ,
Malpighiales	Hypericaceae	<i>Vismia cayennensis</i>	<i>Lycoderides labyrinthicus</i>
Malpighiales	Hypericaceae	<i>Vismia sessilifolia</i>	<i>Stegaspis fronditia</i>
Malpighiales	Linaceae	<i>Hebepetalum humiriifolium</i>	<i>Enchenopa gladius</i>
Malpighiales	Malpighiaceae	<i>Byrsonima</i> sp.	<i>Erechtia gibbosa</i>
Malpighiales	Malpighiaceae	<i>Byrsonima</i> cf. <i>aerugo</i>	<i>Procyrtia</i>
Malpighiales	Malpighiaceae	<i>Byrsonima crassifolia</i>	<i>Enchenopa</i>
Malpighiales	Malpighiaceae	<i>Heteropterys leona</i>	<i>Amastris</i> , <i>Enchenopa concolor</i>
Malpighiales	Malpighiaceae	<i>Hiraea</i> cf. <i>fagifolia</i>	<i>Amastris</i>
Malpighiales	Salicaceae	<i>Banara guianensis</i>	<i>Hemiptycha obtecta</i> , <i>Bolbonota</i> , <i>Membracis foliatafasciata</i> , <i>Neotynelia</i> , <i>Aphetea</i> , <i>Amastris</i> , <i>Horiola</i> , <i>Todea</i> , <i>Tritropidia</i> , <i>Tropidolomia</i> , <i>Stegaspis fronditia</i> , <i>Harmonides reticulata</i> , <i>Membracis nigra</i> , <i>Membracis tectigera</i> , <i>Hemiptycha cultrata</i> , <i>Bocydium globulare</i> , <i>Cyphonia clavata</i> , <i>Enchenopa concolor</i> , <i>Enchenopa albidorsa</i> , <i>Enchenopa gladius</i>
Malpighiales	Salicaceae	<i>Casearia pitumba</i>	<i>Tropidolomia</i>
Malvales	Bixaceae	<i>Bixa orellana</i>	<i>Neotynelia</i>

Malvales	Malvaceae	<i>Helicteres pentandra</i>	<i>Membracis tectigera</i>, <i>Enchenopa squamigera</i>
Malvales	Malvaceae	<i>Hibiscus tiliaceus</i>	<i>Amastris</i>
Malvales	Malvaceae	<i>Pachira aquatica</i>	<i>Amastris</i> , <i>Horiola</i>
Malvales	Malvaceae	<i>Theobroma cacao</i>	<i>Horiola</i>, <i>Neotynelia</i>
Malvales	Malvaceae	<i>Theobroma grandiflorum</i>	Tragopini , <i>Horiola</i> , <i>Neotynelia</i>
Myrtales	Combretaceae	<i>Combretum</i> cf. <i>rotundifolium</i>	<i>Erechtia</i>
Myrtales	Melastomataceae	/	<i>Lycoderides marginalis</i>, <i>Lycoderides luteus</i>, <i>Lycoderides fernandezi</i>, <i>Lycoderes</i>, <i>Leioscyta</i>, <i>Amastris</i>, <i>Tropidoscyta</i>, <i>Erechtia nigrovittata</i>, <i>Membracis lefebvrei</i>, <i>Darnis lateralis</i>, <i>Stictopelta</i>
Myrtales	Melastomataceae	<i>Miconia alata</i>	<i>Erechtia diminuta</i>
Myrtales	Melastomataceae	<i>Miconia</i> cf. <i>argyrophylla</i>	<i>Erechtia diminuta</i>, <i>Lycoderes marginalis</i>, <i>Membracini</i>, <i>Micrutalis</i>
Myrtales	Melastomataceae	<i>Miconia</i> cf. <i>sagotiana</i>	<i>Amastris</i>
Myrtales	Melastomataceae	<i>Miconia minutiflora</i>	<i>Lycoderides minutifloraphiles</i>, <i>Erechtia diminuta</i>
Myrtales	Melastomataceae	<i>Miconia plukenetii</i>	<i>Amastris</i>
Myrtales	Mimosaceae	<i>Mimosa</i> sp.	<i>Enchenopa concolor</i>
Myrtales	Mimosaceae	<i>Mimosa myriadena</i>	<i>Cymbomorpha amazona</i>
Myrtales	Mimosaceae	<i>Mimosa pigra</i>	<i>Enchenopa gracilis</i>, <i>Membracis foliatafasciata</i>
Myrtales	Onagraceae	<i>Ludwigia</i> sp.	<i>Cyphonia clavata</i>
Myrtales	Vochysiaceae	<i>Erismia</i> cf. <i>floribundum</i>	<i>Tolania</i>
Myrtales	Vochysiaceae	<i>Vochysia</i> cf. <i>neyratii</i>	<i>Membracis</i>
Piperales	Aristolochiaceae	<i>Aristolochia</i> cf. <i>bukuti</i>	<i>Hyphinoe</i>
Piperales	Piperaceae	<i>Peperomia</i>	Membracini , <i>Bolbonota</i>
Piperales	Piperaceae	<i>Piper</i> sp.	<i>Enchenopa</i>, <i>Tritropidia</i>, <i>Lophyraspis muscaria</i>, Tragopini, <i>Bolbonota</i>

Poales	Bromeliaceae	<i>Catopsis berteroniana</i>	<i>Enchenopa</i>
Poales	Bromeliaceae	<i>Pitcairnia cremersii</i>	<i>Enchenopa</i>
Poales	Cyperaceae	<i>Scleria secans</i>	<i>Stylocentrus ancora</i>
Poales	Poaceae	/	<i>Trichaetipyga infantilis</i>
Rosales	Cannabaceae	<i>Cannabis sativa</i>	<i>Cyphonia clavata</i>
Rosales	Cannabaceae	<i>Celtis iguanea</i>	<i>Stictopelta</i>
Rosales	Cannabaceae	<i>Trema micrantha</i>	<i>Membracis foliatafasciata</i>, <i>Enchenopa anseriformis</i>, <i>Membracis tectigera</i>, <i>Membracis foliataarcuata</i>, <i>Membracis dorsata</i>, <i>Enchenopa albidorsa</i>, <i>Cyphonia clavata</i>, <i>Bocydium globulare</i>
Rosales	Moraceae	/	<i>Procyrtia</i>
Rosales	Moraceae	<i>Artocarpus altilis</i>	<i>Cyphonia clavata</i>
Rosales	Moraceae	<i>Artocarpus heterophyllus</i>	<i>Cyphonia clavata</i>
Rosales	Moraceae	<i>Ficus</i> sp.	<i>Bolbonota</i>, <i>Aetalion reticulatum</i>, <i>Membracis tectigera</i>
Rosales	Rhamnaceae	<i>Gouania</i> cf. <i>lupuloides</i>	<i>Ceresa distans</i>
Rosales	Urticaceae	<i>Cecropia sciadophylla</i>	<i>Membracis</i>
Rosales	Urticaceae	<i>Pourouma</i> sp.	<i>Phyllotropis fasciata</i>, <i>Membracis</i>, <i>Hypsoprora bifida</i>, <i>Tritropidia nimbata</i>
Sapindales	Anacardiaceae	<i>Anacardium occidentale</i>	<i>Guayaquila</i>, <i>Bolbonota</i>
Sapindales	Anacardiaceae	<i>Spondias mombin</i>	<i>Tragopini</i>, <i>Chelyoidea</i>
Sapindales	Anacardiaceae	<i>Tapirira</i> cf. <i>guianensis</i>	<i>Neotynelia</i>, <i>Phormophora maura</i>
Sapindales	Anacardiaceae	<i>Mangifera indica</i>	<i>Bolbonota</i>, <i>Havilandia pruinosa</i>
Sapindales	Sapindaceae	<i>Paullinia</i> sp.	<i>Notocera</i> spp., <i>Hypsoprora bifida</i>
Sapindales	Sapindaceae	<i>Paullinia</i> cf. <i>pinnata</i>	<i>Rhexia</i>
Sapindales	Sapindaceae	<i>Paullinia rubiginosa</i>	<i>Rhexia</i>

Solanales	Convolvulaceae	/	<i>Abelus</i>
Solanales	Solanaceae	<i>Markea longiflora</i>	<i>Tritropidia nimbata</i> , <i>Bolbonota</i> , <i>Hemiptycha obtecta</i>
Solanales	Solanaceae	<i>Solanum</i>	<i>Amblyophallus</i> , <i>Enchenopa gracilis</i> , <i>Enchenopa squamigera</i> , <i>Neotynelia</i>
Solanales	Solanaceae	<i>Solanum jamaicense</i>	<i>Amblyophallus</i>
Solanales	Solanaceae	<i>Solanum leucocarpon</i>	<i>Eunusa</i> , <i>Alobia</i> , <i>Anobilia</i> , <i>Tragopa</i> , <i>Horiola</i> , <i>Amastris obtegens</i> , <i>Membracis foliatafasciata</i> , <i>Hemiptycha cultrata</i> , <i>Harmonides reticulata</i> , <i>Stegaspis fronditia</i> , <i>Bolbonota</i> , <i>Lycoderes fabricii</i> , <i>Enchenopa squamigera</i> , <i>Cyphonia clavata</i> , <i>Abelus luctuosus</i>
Solanales	Solanaceae	<i>Solanum rugosum</i>	<i>Bolbonota</i> , <i>Tritropidia</i> , <i>Aphetea</i> , <i>Bocydium globulare</i> , <i>Amastris obtegens</i> , <i>Hemiptycha obtecta</i> , <i>Cyphonia clavata</i>
Solanales	Solanaceae	<i>Solanum schlechtendalianum</i>	<i>Amastris</i>
Solanales	Solanaceae	<i>Solanum velutinum</i>	<i>Amblyophallus exaltatus</i>
Solanales	Solanaceae	<i>Solanum endopogon</i>	<i>Alobia</i>

Table 2. Mutualistic Interactions Between Membracids and Hymenoptera.

Membracid species found in ant shelters are shown in **bold**.

Ants				Membracides
Family	Sub-family	Tribe	Genus or species	Genus or species
Apidae	Meliponinae	Meliponini	<i>Trigona</i>	<i>Anchistrotus</i> , <i>Enchenopa concolor</i> , <i>Erechtia nigrovittata</i>
Formicidae	Dolichoderinae	Dolichoderini	<i>Dolichoderus</i>	<i>Colisicostata scutellaris</i> , <i>Membracis foliatafasciata</i> , <i>Bolbonota</i> , <i>Stictopelta</i> , <i>Aphetea</i> , <i>Hemiptycha cultrata</i> , <i>Hemiptycha oblecta</i> , <i>Guayaquila xiphias</i> , <i>Tropidolomia</i> , <i>Enchenopa squamigera</i> , <i>Neotynelia</i> , <i>Anchistrotus</i> , <i>Tropidaspis</i> , <i>Erechtia nigrovittata</i> , <i>Erechtia diminuta</i> , <i>Anobilia</i> , <i>Enchenopa concolor</i> , <i>Notocera cruciata</i>
Formicidae	Dolichoderinae	Dolichoderini	<i>Dolichoderus attelaboides</i>	<i>Horiola</i> , <i>Neotynelia</i> , <i>Erechtia nigrovittata</i>
Formicidae	Dolichoderinae	Dolichoderini	<i>Dolichoderus bidens</i>	<i>Heteronotus horridus</i> , <i>Tropidolomia auriculata</i> , <i>Guayaquila xiphias</i>
Formicidae	Dolichoderinae	Dolichoderini	<i>Dolichoderus bispinosus</i>	<i>Lophyraspis</i>
Formicidae	Dolichoderinae	Dolichoderini	<i>Dolichoderus debilis</i>	<i>Membracis foliatafasciata</i> , <i>Anchistrotus</i>
Formicidae	Ectatomminae	Ectatommini	<i>Ectatomma brunneum</i>	<i>Membracis foliatafusca</i>
Formicidae	Ectatomminae	Ectatommini	<i>Ectatomma tuberculatum</i>	<i>Anchistrotus</i> , <i>Darnis lateralis</i> , <i>Membracis tectigera</i> , <i>Membracis foliatafusca</i> , <i>Membracis foliatafasciata</i> , <i>Membracis lefebvrei</i> , <i>Lycoderides marginalis</i> , <i>Phyllotropis fasciata</i> , <i>Tropidaspis</i> , <i>Rhexia</i> , <i>Horiola</i> , <i>Notocera cruciata</i> , <i>Leioscyta</i> , <i>Amastris obtegens</i> , <i>Notogonoides costigerus</i> , <i>Siegaspis fronditia</i> , <i>Tritropidia</i> , <i>Heteronotus horridus</i> , <i>Horiola</i> , <i>Erechtia nigrovittata</i> , <i>Tropidaspis</i> , <i>Enchenopa albidorsa</i> , <i>Enchenopa concolor</i> , <i>Enchenopa squamigera</i>
Formicidae	Formicinae	Camponotini	<i>Camponotus</i>	<i>Erosne</i> , <i>Erechtia diminuta</i> , <i>Membracis</i> , <i>Lophyraspis</i> , <i>Anchistrotus</i> , <i>Enchenopa</i> , <i>Aphetea</i> , <i>Horiola</i> , <i>Tritropidia nimbata</i> , <i>Tragopa corniculata</i> , <i>Aetalion reticulatum</i>
Formicidae	Formicinae	Camponotini	<i>Camponotus brevis</i>	<i>Enchenopa concolor</i>
Formicidae	Formicinae	Camponotini	<i>Camponotus rufipes</i>	<i>Stictopelta squara</i> , <i>Membracis tectigera</i>
Formicidae	Formicinae	Camponotini	<i>Camponotus sexguttatus</i>	<i>Bolbonota</i>
Formicidae	Myrmicinae	Attini	<i>Daceton armigerum</i>	<i>Guayaquila</i> , <i>Heteronotus</i> , <i>Membracis foliatafusca</i> , <i>Membracis foliatafasciata</i>
Formicidae	Myrmicinae	Attini	<i>Pheidole</i>	<i>Bolbonota</i> , <i>Tragopa annulata</i> , <i>Horiola</i> , <i>Heteronotus spinosus</i> , <i>Tragopa</i> , <i>Anobilia</i>
Formicidae	Myrmicinae	Cephalotini	<i>Cephalotes</i>	<i>Membracis</i> , <i>Nicomini</i>
Formicidae	Myrmicinae	Cephalotini	<i>Cephalotes atratus</i>	<i>Phormophora maura</i> , <i>Enchenopa concolor</i> , <i>Lycoderides brulei</i> , <i>Anchistrotus</i> , <i>Todea</i> , <i>Erechtia</i> , <i>Membracini</i>
Formicidae	Myrmicinae	Crematogastrini	<i>Crematogaster</i>	<i>Amastris obtegens</i> , <i>Dioclophara viridula</i> , <i>Rhexia</i> , <i>Harmonides reticulata</i> , <i>Anchistrotus</i> , <i>Stylocentrus ancora</i> , <i>Enchenopa concolor</i> , <i>Stictocephala</i> , <i>Endoiastini</i> , <i>Tragopa</i> , <i>Notocera cruciata</i> , <i>Membracis foliatafasciata</i> , <i>Membracis nigra</i>
Formicidae	Myrmicinae	Myrmicini	/	<i>Folicarina bicolor</i>
Formicidae	Myrmicinae	Myrmicini	<i>Azteca</i>	<i>Harmonides</i>, <i>Chelyoidea</i>, <i>Amastris</i>, <i>Rhexia</i>, <i>Tritropidia</i>
Formicidae	Myrmicinae	Solenopsidini	<i>Megalomyrmex</i>	<i>Hypsoprora bifida</i> , <i>Anchistrotus</i> , <i>Chelyoidea</i> , <i>Phyllotropis fasciata</i> , <i>Membracis</i>
Formicidae	Myrmicinae	Solenopsidini	<i>Solenopsis</i>	<i>Enchenopa gracilis</i> , <i>Bolbonota</i>
Formicidae	Myrmicinae	Solenopsidini	<i>Solenopsis saevissima</i>	<i>Membracis</i>
Formicidae	Ponerinae	Ponerini	<i>Odontomachus</i>	<i>Enchenopa</i> , <i>Membracis</i>

Table 3. Degree of affinity of different tribes of Membracidae with ants.

Mutual interactions	Tribe or sub-family
Unknown	Centronodinae, Acutalini, Micrutalini, Microcentrini
None	Darnini, Cymbomorphini, Hemikypthini, Boocerini, Hoplophorionini, Nicomiini, Ceresini
Rare	Procyrtini, Hypsoprurini
Occasional	Endoiastini, Stegaspidini
Frequent	Heteronotini, Aconophorini, Membracini, Talipedini, Amastrini, Polyglyptini
Always	Tragopini, Aetalionidae

Table 4. Main mimetic strategies for membracides.

Plant	<i>Cymbomorpha</i> , <i>Germariana</i> , <i>Nassunia</i> , <i>Heteronotus delineatus</i> , <i>Aconophora</i> , <i>Guayaquila</i> , <i>Tropidoscyta</i> , <i>Paragara</i> , <i>Erechtia</i> , <i>Havilandia</i> , <i>Leioscyta</i> , <i>Potnia</i> , <i>Umbonia</i> , <i>Ochropepla</i> , <i>Hypsoprora</i> , <i>Philya</i> , <i>Cladonota</i> , <i>Ceresa</i> , <i>Eumela</i> , <i>Dioclophara</i> , <i>Notogonioides</i> , <i>Ramedia</i> , <i>Aphetea</i> , <i>Aurismastris</i> , <i>Amastris</i> , <i>Erosne</i> , <i>Stylocentrus</i> , <i>Lycoderides</i> , <i>Lycoderes</i> , <i>Hebetica</i> , <i>Calloconophora</i> , <i>Pseuderechthia</i> , <i>Talipes</i> , <i>Vanduzea</i> , <i>Stictopelta</i> , <i>Dectonura</i> , <i>Hygris</i> , <i>Enchenopa</i> , <i>Hemiptycha</i> , <i>Paracentronodus</i> , <i>Centronodus</i> , <i>Tolania</i> , <i>Tumecauda</i> , <i>Flexocentrus</i> , <i>Anchistotrus</i> , <i>Smerdalea</i> , <i>Stegaspis</i>
Droppings	<i>Aspona</i> , <i>Hypheodana</i> , <i>Bolbonota</i>
Formicidae / Vespidae	<i>Heteronotus</i> , <i>Cyphonia</i>
Formicidae (partial)	<i>Tropidolomia</i> , <i>Tragopa</i> , <i>Todea</i> , <i>Anobilia</i> , <i>Guayaquila</i> (L)
Aposematic	<i>Darnis</i> , <i>Enchophyllum</i> , <i>Membracis</i> , <i>Folicarina</i> , <i>Tritropidia</i> , <i>Smilidarnis</i> , <i>Harmonides</i> , <i>Chelyoidea</i> , <i>Notogonioides</i> (L), <i>Neotynelia</i> (L)
Undetermined	<i>Hemikyptha</i> , <i>Alcmeone</i> , <i>Atypa</i> , <i>Hyphinoe</i> , <i>Procyrta</i> , <i>Sundarion</i> , <i>Stictodepsa</i> , <i>Scytodepsa</i> , <i>Alodrillus</i> , <i>Smiliorachis</i> , <i>Rhexia</i> , <i>Notocera</i> , <i>Phormophora</i> , <i>Thuris</i> , <i>Micrutalis</i> , <i>Thrasymedes</i> , <i>Neotynelia</i> , <i>Tynelia</i> , <i>Nicomia</i> , <i>Horiola</i> , <i>Oeda</i> , <i>Umbelligerus</i> , <i>Bocyidium</i> , <i>Endoiastus</i> , <i>Eunusa</i> , <i>Hypsoprora</i> , <i>Notocera</i> , <i>Cladonota</i> , <i>Abelus</i> , <i>Ischnocentrus</i> , <i>Lallemandia</i> , <i>Funkhouseriana</i> , <i>Nasuconia</i> , <i>Chelyoidea</i>

Table 5. Morphological classification of genera.

Helmet morphology	Genus or species
One posterior projection developed into a spine	<i>Cymbomorpha</i> , <i>Germariana</i> , <i>Paragara</i> , <i>Erechtia</i> , <i>Eumela</i> , <i>Hebetica</i> , <i>Pseuderechtia</i> , <i>Talipes</i> , <i>Stictopelta</i> , <i>Dectonura</i> , <i>Hygris</i> , <i>Paracentronodus</i> , <i>Hypheodana</i> , <i>Funkhouseriana</i> , <i>Darnis</i> , <i>Procyrtia</i> , <i>Alodrillus</i> , <i>Smiliorachis</i> , <i>Thuris</i> , <i>Micrutalis</i> , <i>Thrasymedes</i> , <i>Hyphinoe</i> , <i>Smilidarnis</i>
One anterior horn and one posterior projection	<i>Aconophora</i> , <i>Guayaquila</i> , <i>Potnia</i> , <i>Umbonia</i> , <i>Notogonioides</i> , <i>Calloconophora</i> , <i>Enchenopa</i> , <i>Hemiptycha</i> , <i>Enchophyllum</i> , <i>Philya</i>
Two supra-humeral projections	<i>Nassunia</i> , <i>Ceresa</i> , <i>Centronodus</i> , <i>Tumecauda</i> , <i>Flexocentrus</i> , <i>Hemikyptha</i> , <i>Procyrtia</i> , <i>Sundarion</i> , <i>Notocera</i> , <i>Alcmeone</i> , <i>Tolania</i> , <i>Todea</i> , <i>Tropidolomia</i>
Complex multispinous	<i>Cyphonia</i> , <i>Umbelligerus</i> , <i>Smerdalea</i> , <i>Stylocentrus</i> , <i>Bocyidium</i> , <i>Heteronotus</i>
Other: reduced projection, no spine	<i>Abelus</i> , <i>Aspona</i> , <i>Anobilia</i> , <i>Bolbonota</i> , <i>Tropidoscyta</i> , <i>Lallemandia</i> , <i>Vanduzee</i> , <i>Havilandia</i> , <i>Leioscyta</i> , <i>Nasuconia</i> , <i>Chelyoidea</i> , <i>Ochropepla</i> , <i>Dioclophara</i> , <i>Harmonides</i> , <i>Ramedia</i> , <i>Aphetea</i> , <i>Aurismastris</i> , <i>Amastris</i> , <i>Erosne</i> , <i>Tritropidia</i> , <i>Rhexia</i> , <i>Eunusa</i> , <i>Phormophora</i> , <i>Stictodepsa</i> , <i>Scytodepsa</i> , <i>Neotynelia</i> , <i>Tynelia</i> , <i>Nicomia</i> , <i>Horiola</i> , <i>Endoiastus</i> , <i>Ischnocentrus</i>
Developed projection	<i>Cladonota</i> , <i>Hypsoprora</i> , <i>Lycoderides</i> , <i>Lycoderes</i> , <i>Membracis</i> , <i>Folicarina</i> , <i>Phyllotropis</i> , <i>Oeda</i> , <i>Stegaspis</i> , <i>Atypa</i> , <i>Anchistotrus</i>

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Illustration de la couverture :

Larves et adultes de *Erechtia nigrovittata* (Membracidae) en interaction avec *Dolichoderus attelaboides* (Formicidae).

Crédits:

Jérémie Lapèze : Fig. 1-7 & couverture.